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Tastes of salts and acids on circumvallate papillae and anterior tongue[1]

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Abstract. In a psychophysical study with human subjects, three chloride salts and three acids were tasted at two different isointense concentrations. Subjects profiled the taste sensations elicited when the stimuli were applied to small regions of the anterior tongue and to individual circumvallate papillae. The results extended earlier findings showing systematic differences in the responses to acids and salts as a function of the locus to which a stimulus is applied. All salts were perceived as predominantly salty on the anterior tongue, and as predominantly sour or bitter on circumvallate papillae, although there was a weak salty component in the response to lower concentrations of salt on circumvallate papillae. Acids were perceived as sour on circumvallate papillae, and as sour and salty on the anterior tongue. Cationic atomic weight was positively related to saltiness on both loci. However, while salts apparently stimulate both bitter and sour receptors on both the anterior tongue and circumvallate papillae, there was no systematic relationship between cationic atomic weight and the magnitude of the sour and bitter tastes elicited. It was concluded that the possibility of unequal distributions of receptor types between fungiform and circumvallate regions should be taken into account when interpreting the results of experiments using whole-mouth stimulation with salts and acids.

Introduction

When human subjects taste salt solutions with the whole mouth, they report each of the four basic tastes systematically as a function of concentration and species of ionic solution (e.g. von Skramlik, 1926; Dzendolet and Meiselman, 1967; Cardello and Murphy, 1977; Murphy *et al.*, 1981; McBurney and Shick, 1971). The atomic weights of both the cation and anion have been correlated with the salty and bitter tastes of salts. The heavier ions of both electrostatic charges are associated with increased bitterness, whereas the lighter anions are associated with greater saltiness (Murphy *et al.*, 1981), presumably due to the fact that heavier anions are more inhibitory of the salty taste than are lighter anions (Beidler, 1954).

The taste of salts appears to be a complex function of interactions among tastes as well. For example, in experiments wherein the receptors coding saltiness are adapted by prolonged exposure to salt, there is an accompanying increase in the sour and bitter tastes of the salts (Bartoshuk *et al.*, 1964; Murphy *et al.*, 1981). The perceptual explanation of this phenomenon is that under normal circumstances, the salty taste suppresses or masks the other tastes produced by salt stimuli. The physico-chemical explanation is that adaptation to salts changes the ion-pair formation rate, allowing negative ions to approach the receptor membrane, thereby permitting increased stimulation of bitter receptors (DeSimone and Price, 1976).

In the case of acids, a less complex hypothesis has been proposed to explain the mechanisms responsible for the sour taste (Beidler, 1967, 1971). According to this hypothesis, the H^+ cation is the excitatory ion for the receptor. However, because pH is not a direct predictor of the sourness of any particular acid compound (Moskowitz, 1971), more complex theories (Makhlouf and Blum, 1972; Price and DeSimone, 1977) have been elaborated and tested. The anions are believed to indirectly facilitate the sour taste by decreasing the positive charge on the membrane that is produced by the binding of the H^+ ions to the receptor.

The possibility that receptors which respond to salt and acid compounds on the front of the tongue differ from those on circumvallate papillae was raised by some of our earlier studies (Sandick and Cardello, 1981). To the majority of human subjects, NaCl tastes sour, bitter, or both when the stimulus solution is applied to individual circumvallate papillae, whereas it tastes primarily salty (or sour) on the anterior tongue. Similar non-characteristic responses have been shown to occur when citric acid is applied to the anterior tongue, where it has been reported to taste sour and/or salty (Cardello, 1979; Kuznicki, 1978; Nilsson, 1979). In contrast, citric acid tastes predominantly sour on circumvallate papillae (Sandick and Cardello, 1981). In an attempt to determine whether the findings of our earlier experiments generalize to other salts and acids, a variety of acids and simple chloride salts were tested on the two tongue loci.

Method

Subjects

Ten female and ten male subjects participated in the experiment. All were employees of the US Army Natick Laboratories and four of the 20 subjects reported themselves to be moderate or light cigarette smokers. Subjects ranged in age from 18 to 48 yr. About 20% of volunteers were eliminated from participation, because their circumvallate papillae were not clearly visible or accessible.

Apparatus and procedure

The techniques for stimulating circumvallate papillae and small areas of the anterior tongue were those described in a previous report (Sandick and Cardello, 1981). Subjects were seated comfortably at a small experimental table. An adjustable U-shaped metal chin rest was used to tilt the subject's head backward at a 20° angle. Blunt, 30-gauge, stainless steel hypodermic needles (3.8 cm shaft length) attached to 1 ml tuberculin syringes were used to produce 0.25 μl droplets of the stimulus solutions. One droplet was used to stimulate either the anterior tongue or a single circumvallate papillae. During trials on which the stimulus was placed on the anterior tongue, the subject extended his tongue and rested it on his lower lip. In order to place droplets on a single circumvallate papilla, the shaft of each hyperdermic needle was disposed at a 45° angle at a location that was 1 cm from the tip. Subjects opened their mouths as wide as possible (within comfortable limits), extended the tongue, and maintained it in a stationary position by applying gentle pressure on the tip of the tongue with a cloth moistened in distilled water. This tactile stimulation of the anterior tongue was assumed to produce no effect upon the taste sensations of the posterior tongue. Each droplet was released from the tip of the needle upon contact with the lingual surface.

A repeated measures design on all factors was employed. Each subject received all solutions once in random order to random regions of the anterior tongue, and then once in random order to a single circumvallate papilla of the left or right side. The order of presentation to each region was not counterbalanced because subjects were required to apply gentle pressure on the front of the tongue during stimulation of circumvallate papillae. It was felt that after this tactile stimulation the responses on the anterior tongue may have been affected temporarily. Two circumvallate papillae were stimulated in each subject. Thus, a total of 40 individual circumvallate papillae were stimulated in this experiment.

Subjects gave a numerical estimate of the overall intensity elicited by the first stimulus solution and divided that estimate among the four basic taste qualities and an 'other' category. Subjects rated all subsequent intensities in proportion to the intensity evoked by the first solution (McBurney and Bartoshuk, 1973; Kuznicki, 1978).

Subjects rinsed with distilled water between trials. While the interstimulus interval between consecutive trials was ~45 s, sequential stimuli in the series were always presented to distant lingual areas (or papillae), so that the effective interstimulus interval for any particular area (or papilla) was longer than 45 seconds.

Stimuli

Three salts (NaCl, LiCl, and KCl) and three acids (HCl, citric and L-ascorbic) were used in the experiment. Choice of the particular salts was made on the basis of the fact that each had been shown to produce a different characteristic taste with whole-mouth procedures. When tasted with the whole-mouth, NaCl is the saltiest-tasting salt, whereas LiCl has a significant sour component, and KCl a significant bitter component (Renqvist, 1919; von Skramlik, 1926; Dzendolet and Meiselman, 1967; Cardello and Murphy, 1977; Murphy *et al.*, 1981). The acid compounds were chosen to include an inorganic (HCl) and two organic acids commonly found in foods (citric and L-ascorbic).

The concentrations of the test compounds used in the experiment were determined by a 'sip and spit' matching procedure with 12 subjects. Subjects rinsed with distilled water between solutions. High (30 mM) and low (10 mM) concentrations of HCl were chosen as reference stimuli. Dilutions of citric and ascorbic acid were tasted by the subjects in a bracketing procedure. Subjects tasted one of the reference stimuli and one of the test acids and judged their relative intensities. The experimenter chose the next stimulus for presentation based upon the subject's response, until a match was approximated. The same procedure was used for NaCl, LiCl, and KCl. Subjects were instructed to consider only the intensity of the taste sensations, without regard to the quality of the tastes, i.e., sour or salty. In such a fashion, concentrations were determined for each of the salts and the organic acids which approximated 10 and 30 mM HCl in overall taste intensity. The concentrations employed in the experiment are shown in Table I. The lower concentration of each compound was the average of all subjects' matches to 10 mM HCl and the higher concentration was the average match to 30 mM HCl.

Table I. Concentrations (mM) of solutions used in the experiment

HCl	Citric acid	Ascorbic acid	NaCl	LiCl	KCl
10	10	25	250	250	250
30	35	60	1000	1000	400

All solutions were tested at room temperature, stored in a refrigerator (6°C) when not in use, and made with reagent grade chemicals and triple-deionized water. Organic acid solutions were mixed weekly.

Pretesting and training for taste identification

To facilitate interpretation of results, it was necessary to ensure that all subjects were using taste names in a consistent manner. Many investigators have observed errors in the labeling of the sour and bitter taste qualities due to a lack of subject experience in identifying these tastes (Meiselman and Dzendolet, 1967; McAuliffe and Meiselman, 1974; Robinson, 1970; O'Mahoney *et al.*, 1979; Gregson and Baker, 1973). Since the sour and bitter tastes are salient components of the tastes of acids and salts, a training procedure was undertaken for all subjects who had labeled these tastes inappropriately in a pre-test.

Four solutions were used as screening stimuli: 50 mM NaCl; 0.125 mM quinine sulfate; 25 mM sucrose; and 2 mM HCl. Subjects first rinsed with distilled water, then tasted 5 ml of each solution in random order, and identified the taste quality of each stimulus. Between solutions, subjects rinsed with distilled water. If the subject identified quinine as 'sour' or HCl as 'bitter', the training procedure was implemented. In this procedure, the subject tasted quinine sulfate and one of the test acids and was instructed to name the acid taste 'sour' and the taste of quinine 'bitter'. This procedure was repeated until the subject stated that he or she could discriminate the sour and bitter tastes. After the subject named the solutions correctly in a retest, the experiment began.

Results

Every combination of one, two, three, and four tastes (with the exception of bitter-sour-sweet) was observed at least once with all subjects over the course of the experimental sessions. However, responses composed of only one taste were the most common. There were 120 trials with each class of compound on each locus over all subjects. Of the 120 trials with acids on the anterior tongue, 62% of responses were composed of only one taste quality: 26 salty; 32 sour; 13 bitter; and 4 sweet. Of the 120 trials with salts on the anterior tongue, 64% of responses were composed of only one taste quality: 54 salty; 14 sour; 7 bitter; and 3 sweet.

On the circumvallate papillae, the percentages were similar, with 61% of responses to acids being unitary (5 salty, 44 sour, 18 bitter, and 7 sweet), and 62% of responses to salts being unitary (20 salty, 20 sour, 31 bitter, and 4 sweet).

The most common response composed of two tastes for the anterior tongue was salty-sour, accounting for 10% of responses to acids and 8% of responses to salts. The most common dual response for circumvallate papillae was bitter-sour, accounting for 13% of responses to acids and 4% of responses to salts. No other dual- or triple-quality responses occurred on more thn 5% of trials with either compound on either locus.

The numerical judgments were analyzed, with minor modifications, as reported in an earlier paper (Sandick and Cardello, 1981). For normalization across subjects, the median value for each subject's judgments of overall intensity was calculated. The median, rather than the geometric mean, was used because of the presence of zeroes in the intensity data: 21% (34/160) of responses on the anterior tongue and 14% (23/160) of responses on circumvallate papillae. This median was used as the divisor for all of that subject's numerical judgments. Applied to the data of every subject, this procedure brought the median value for every subject's data to 1.0. Data from all subjects for each solution and locus of stimulation were then combined and a 'weighted geometric mean' was calculated. The geometric mean of the nonzero magnitude estimates was multiplied by the proportion of trials on which the taste quality was reported on that locus with that solution. The results (multiplied by 100 to eliminate fractional values) are plotted as bargraphs in Figure 1 – 4.

Paired t-tests were performed on the data for each solution to determine whether subjects' judgments of overall intensity were significantly different as a function of the locus of stimulation. After accounting for the 12 contrasts by reducing the alpha level to 0.01, the only significant differences between the loci were found for the lowest concentrations of NaCl and LiCl. For these solutions (250 mM NaCl and 250 mM LiCl), intensities on circumvallate papillae were significantly less than intensities on the anterior tongue. Despite the fact that only the intensities of these two solutions were significantly different, 11 of the 12 solutions had lower mean taste intensities on circumvallate papillae than on the anterior tongue. The importance of these intensity differences to the differences in reported taste qualities is a subject for future investigation.

Taste profiles for acids

The three acids at higher and lower concentrations produced similar response profiles on circumvallate papillae (Figure 1). For every acid solution the sour taste predominated. In fact, more than 50% of the responses contained a sour component (percentage data not shown). However, for acids presented to the anterior tongue (Figure 2), marked salty and sour components were also present, with the profiles differing by compound and concentration. Only 35 mM citric acid produced a taste profile in which the sour component was substantially greater than the salty component, in marked contrast to what was observed on circumvallate papillae (Figure 1).

Taste profiles for salts

When salts were applied, the picture was reversed. Now, complex responses were produced on the circumvallate papillae (Figure 3). At the lower concentration, NaCl produced a predominantly salty response, LiCl a very weak mixed response, and KCl a more substantial response involving all taste qualities, with

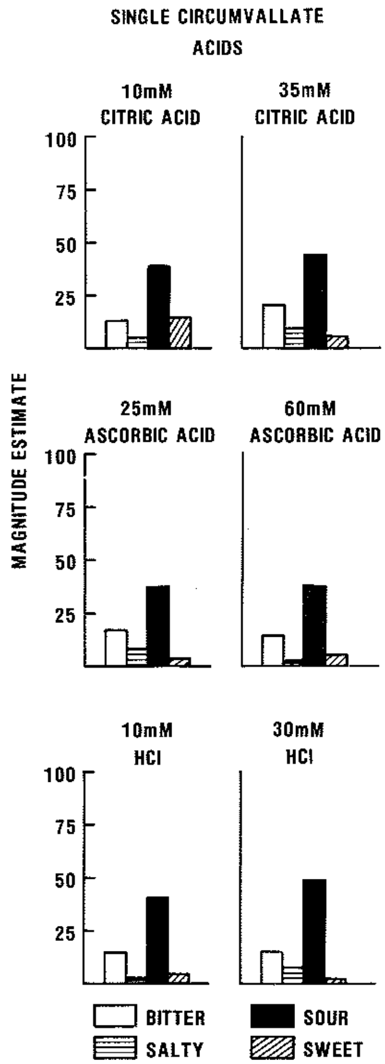

Fig. 1. Weighted geometric mean magnitude estimates of each taste quality for acids on circumvallate papillae.

salty and sour predominating (Figure 3). At the higher concentration the responses were composed primarily of sour and bitter. For all salts, the salty component decreased from lower to higher concentrations.

When salts were applied to the anterior tongue (Figure 4), all salts produced similar taste profiles. The response was intensely salty, with weak bitter and sour components. The sour component of the response to salts on this locus was always less than half of that for the salty component, in contrast to what was observed for these compounds on circumvallate papillae (Figure 3). At the higher

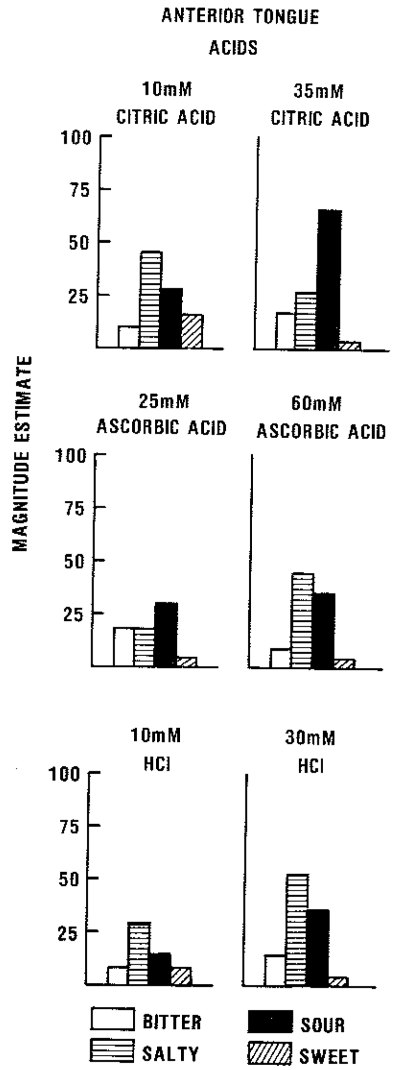

Fig. 2. Weighted geometric mean magnitude estimates of each taste quality for acids on the anterior tongue.

concentrations, the salts increased in saltiness, while the other taste components remained stable.

Discussion

The findings of the present experiment provide more evidence for reliable differences between fungiform and circumvallate papillae in the coding of the tastes of salts and acids. The results of earlier experiments (Sandick and Cardello, 1981; Cardello, 1979) which showed that citric acid elicited salty as well as sour

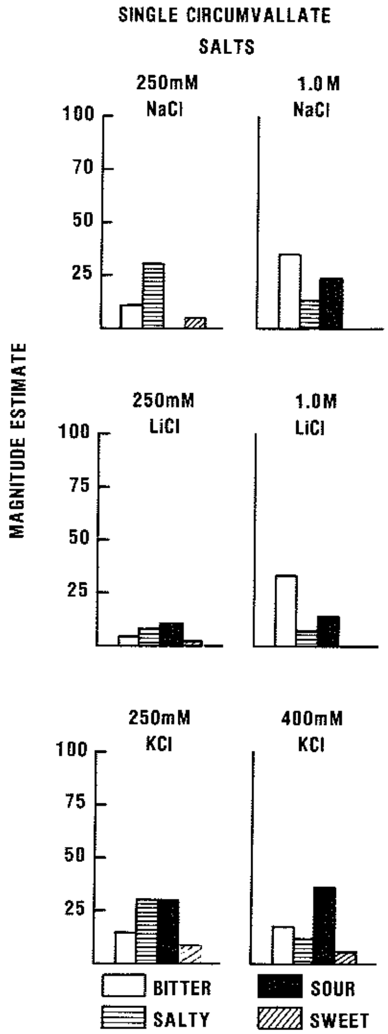

Fig. 3. Weighted geometric mean magnitude estimates of each taste quality for salts on circumvallate papillae.

responses on the anterior tongue generalized in this experiment to hydrochloric and ascorbic acids (Figure 2). Similarly, the bitter and sour taste profile found for NaCl on circumvallate papillae in earlier experiments (Sandick and Cardello, 1981) was also found for LiCl and KCl. Much of these results can be explained by proposing that (1) there is an uneven distribution of receptors coding saltiness across the lingual surface, with a greater density found in anterior regions than in circumvallate regions, (2) that, in addition to exciting salty receptors, many salts excite sour and bitter receptors on the two loci, and (3) that, in addition to exciting sour receptors, many acids excite receptors coding saltiness.

There were, however, some inconsistencies between these results and those of

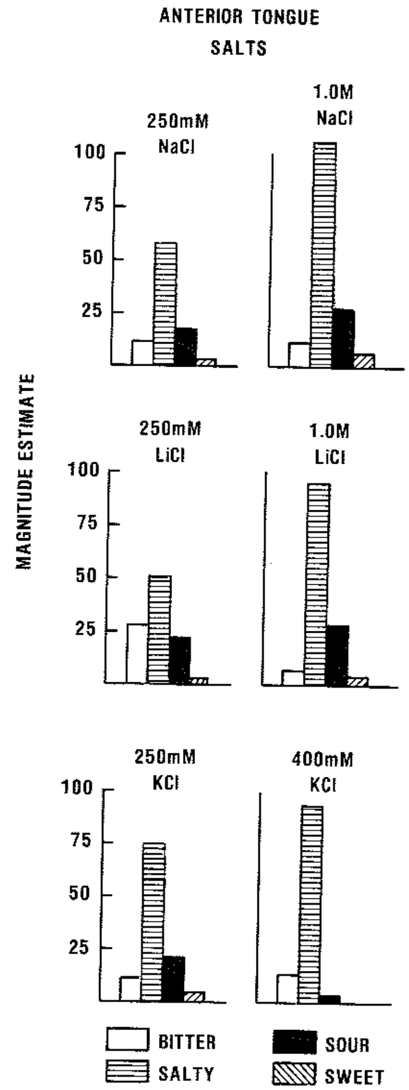

Fig. 4. Weighted geometric mean magnitude estimates of each taste quality for salts on the anterior tongue.

an earlier experiment (Sandick and Cardello, 1981). Similar taste profiles for NaCl and citric acid had been produced with stimulation of the anterior tongue in the earlier experiment. However, no attempt had been made to equate the overall intensities of the solutions. When the overall taste intensities of the solutions were equated in the present experiment, the taste profiles for the two compounds were substantially different on the anterior tongue. (See profiles for citric acid in Figure 2 and for NaCl in Figure 4.) The concentrations of citric acid and NaCl used in the earlier experiment were so concentrated (0.125 and 5.0 M, respectively) that the elicited responses might have represented an upper limit of the stimulating ability for these compounds on the relevant receptors. At this ceiling of responding, citric acid and NaCl produced similar taste profiles on the anterior tongue. However, the lower concentrations used in the present experiment permitted differences between the tastes of the compounds on the anterior tongue to become apparent.

Since the salts tested differed in cationic (but not anionic) character, some assessment of the effect of cationic atomic weight on the taste profiles can be made. Unfortunately, the represented range of cationic weights in this experiment was ony 6:3:1 (K:Na:Li). Consistent with the theory that cationic atomic weight is positively associated with saltiness, NaCl was perceived as saltier than LiCl at both concentrations on both loci. Also, KCl was perceived to be as salty as NaCl and LiCl on both loci at 250 mM. Similarly, on both loci, KCl at 400 mM approached the saltiness of NaCl and LiCl at 1.0 M. Therefore, it can be stated that the weight of the cations was positively related to saltiness on both regions.

The weight of the cation was a poor predictor of the sour and bitter tastes of salts in this experiment. For example, at the lower concentrations, LiCl was more bitter than NaCl on the anterior tongue (Figure 4) and less bitter on the circumvallate papillae (Figure 3). Similarly, KCl at 400 mM was more sour than either 1.0 M NaCl or LiCl on circumvallate papillae (Figure 3) but less sour than either on the anterior tongue (Figure 4).

The finding that saltiness decreased from low to high salt concentrations on circumvallate papillae (Figure 3) suggests that some other process may be involved than the direct stimulation of receptors coding saltiness. One such process is the 'water taste' (Bartoshuk, 1968), which occurs when water or a less concentrated solution is tasted after preadaptation to a sapid solution. Since NaCl is perceived as bitter on circumvallate papillae, the Na^+ or Cl^- ions in saliva may stimulate bitter receptors in circumvallate papillae. Presentation of water or low concentrations of salts may elicit a salty water taste on these papillae, in the same way that bitter compounds have been shown to produce a salty water taste during anterior tongue stimulation (McBurney and Bartoshuk, 1973). Studies of the phenomenon of water taste are usually accomplished with whole-mouth procedures or with a flow procedure on the anterior dorsal tongue. Studies of water taste phenomena have not been investigated as a function of locus of stimulation. The taste quality differences observed in the present experiments suggest that the examination of water taste in circumvallate regions might produce revealing information about the nature of water taste phenomena.

An important implication of these results is that experiments which investigate the taste of salts using whole-mouth procedures are studying perceptual phenomena involving patterns of stimulation and integration across a varied distribution of receptors. Psychophysical models assuming one-to-one chemical relationships between the stimulus and a uniform distribution of invariant receptors may produce inadequate theories of the stimulating properties of salts.

Footnotes

[1]This experiment was submitted as part of a dissertation by the first author in par-

tial fulfillment of the degree of Doctor of Philosophy at Brandeis University. The interpretations in this paper are not to be construed as an official Department of the Army policy or position.

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